

2021

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10.1029/2021GB006935

Mazarrasa, I., Lavery, P., Duarte, C. M., Lafratta, A., Lovelock, C. E., Macreadie, P. I., ... & Serrano, O. (2021). Factors determining seagrass Blue Carbon across bioregions and geomorphologies. *Global Biogeochemical Cycles*, 35 (6), e2021GB006935. <https://doi.org/10.1029/2021GB006935>

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Global Biogeochemical Cycles

RESEARCH ARTICLE

10.1029/2021GB006935

Key Points:

- Australian seagrasses contain higher soil organic carbon stocks than adjacent unvegetated areas due to higher seagrass inputs
- Seagrass soil carbon stocks are similar over bioregions and geomorphic settings but higher in larger species compared to smaller species
- Factors determining seagrass soil carbon stocks differ across bioregions and coastal geomorphic settings within bioregions

Supporting Information:

Supporting Information may be found in the online version of this article.

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Citation:

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





Received 4 JAN 2021

Accepted 14 MAY 2021

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Factors Determining Seagrass Blue Carbon Across Bioregions and Geomorphologies

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Abstract Seagrass meadows rank among the most significant organic carbon (C_{org}) sinks on earth. We examined the variability in seagrass soil C_{org} stocks and composition across Australia and identified the main drivers of variability, applying a spatially hierarchical approach that incorporates bioregions and geomorphic settings. Top 30 cm soil C_{org} stocks were similar across bioregions and geomorphic settings (min-max: 20–26 Mg C_{org} ha⁻¹), but meadows formed by large species (i.e., *Amphibolis* spp. and *Posidonia* spp.) showed higher stocks (24–29 Mg C_{org} ha⁻¹) than those formed by smaller species (e.g., *Halodule*, *Halophila*, *Ruppia*, *Zostera*, *Cymodocea*, and *Syringodium*; 12–21 Mg C_{org} ha⁻¹). In temperate coastal meadows dominated by large species, soil C_{org} stocks mainly derived from seagrass C_{org} (72 ± 2%), while allochthonous C_{org} dominated soil C_{org} stocks in meadows formed by small species in temperate and tropical estuarine meadows (64 ± 5%). In temperate coastal meadows, soil C_{org} stocks were enhanced by low hydrodynamic exposure associated with high mud and seagrass C_{org} contents. In temperate estuarine meadows, soil C_{org} stocks were enhanced by high contributions of seagrass C_{org} , low to moderate solar radiation, and low human pressure. In tropical estuarine meadows formed by small species, large soil C_{org} stocks were mainly associated with low hydrodynamic energy, low rainfall, and high solar radiation. These results showcase that bioregion and geomorphic setting are not necessarily good predictors of soil C_{org} stocks and that site-specific estimates based on local environmental factors are needed for Blue Carbon projects and greenhouse gases accounting purposes.

1. Introduction

Seagrass meadows are critical coastal ecosystems that support biodiversity, fisheries, regulation of water quality, coastal protection as well as recreational and cultural values (Barbier et al., 2011). In addition, they have been identified as one of the most significant natural carbon sinks on earth, due to their extensive distribution (i.e., along the coast of all continents except the Antarctica; Hemminga & Duarte, 2000), high primary productivity, and rates of carbon burial (Duarte et al., 2005, 2013; Mateo et al., 1997). Around 98% of the C_{org} sequestered in seagrass meadows is stored in the soil compartment, with only 2% allocated to plant above-ground biomass (Serrano et al., 2019). C_{org} sequestered in the soils is derived from senescent above-ground and below-ground biomass and allochthonous C_{org} trapped from the water column by the seagrass canopy, which enhances sedimentation and reduces resuspension (Gacia & Duarte, 2001; Kennedy et al., 2010). Hence, most studies of seagrass Blue Carbon have focused on the soil compartment and the factors influencing soil stocks and accumulation rates.

Table 1

Compilation of Biotic and Abiotic Drivers and Mechanisms Involved in the Variation of Seagrass Soil Organic Carbon (C_{org}) Storage Based on the Most Recent Literature on Blue Carbon and Seagrass Ecology

Spatial scale	Factors of soil C_{org} variability	Mechanisms	Effect in soil C_{org} stocks	Reference
Local	Meadow properties			
	Species composition	Determine below- and above ground biomass, refractory nature of the seagrass debris and the efficiency at enhancing the sedimentation of allochthonous C_{org} .	Large species develop higher stocks	Serrano et al., 2019
	Water depth	Decrease in seagrass productivity due to limited irradiance. Can reduce exposure to hydrodynamic energy and enhance depositional conditions.	↑↓	Serrano et al., 2014; Lavery et., 2013; York et al., 2018
	Hydrodynamic energy	Enhanced export and erosion with increased energy.	↓	Röhr et al. 2016; Samper-Villarreal et al. 2016; Salinas et al., 2020
	Sediment grain size	Fine sediment content favors C_{org} preservation in seagrass soils by increasing anoxic conditions and protecting organic particles from microbial organic matter mineralization.	↑	Mayer 1994; Burdige 2007; Miyajima et al. 2017
	Allochthonous C_{org}	Increase the magnitude of the soil C_{org} deposits.	↑	Ricart et al. 2020; Kennedy et al., 2009
	Habitat geomorphology			
	Coast	Exposed to high hydrodynamic energy from waves, tides and currents, enhancing C_{org} erosion and export.	↓	Carruthers et al. 2002, 2007
		Subtidal environments up to 40 m: light limitation due to water depth.	↓	Duarte 1991
	Estuary	Low hydrodynamic energy from river and tidal flow: depositional environment.	↑	Depositional environment
Large		Intertidal to shallow depths: exposed to solar radiation, desiccation and high temperatures leading to potential decline in seagrass productivity.	↓	Carruthers et al. 2002, 2007
		Subject to terrigenous and anthropogenic inputs: light limitation due to turbidity, higher accumulation of allochthonous C_{org} , higher exposure to pollution	↑↓	Kilminster et al. 2015, Carruthers et al. 2002, 2007
	Bioregion			
	Tropical vs. Temperate	High precipitation: -Enhance allochthonous C_{org} and fine sediment accumulation. -Enhance turbidity and drops in salinity, compromising seagrass productivity and survival.	↑↓	Ridler et al. 2006; Chollett et al. 2007
		High temperature: -Enhance C_{org} remineralization.	↓	Pedersen et al. 2011
		High solar radiation: -Compensate light limitation: enhance seagrass productivity. -Combined with high temperature and tidal exposure compromises seagrass productivity and survival.	↑↓	Stapel et al., 1997

Note. Factors range from a local scale (meadow properties) to a large scale (habitat geomorphology and bioregion).

Despite the valuable services seagrass meadows provide, they have been negatively affected by human-derived pressures in coastal areas, which have contributed to a global decline in seagrass meadow area, particularly during the late 20th century (Waycott et al., 2009). Although recent evidence points to recovery of seagrass cover in certain regions, such as Europe (de los Santos et al., 2019), seagrass meadows remain vulnerable to anthropogenic disturbances worldwide, including key stressors linked to climate change (Grech et al., 2012; Hossain et al., 2019). Loss of these ecosystems leads to the loss of their C_{org} sink capacity along with the other ecosystem services they provide, and may result in a switch from net C_{org} sinks to net CO_2 sources (Arias-Ortiz et al., 2018; Macreadie et al., 2015; Salinas et al., 2020). The potential of seagrasses as C_{org} sinks and the risk of CO_2 emissions if meadows are lost, opens the opportunity to enhance their conservation and restoration for climate change mitigation purposes (Nellemann et al., 2009).

The rapidly growing body of Blue Carbon literature suggests large variability in seagrass soil C_{org} stocks due to a combination of biotic and abiotic factors acting at different spatial scales (Macreadie et al., 2014; Mazarrasa et al., 2018). At local scales, the magnitude of soil C_{org} deposits has been related to seagrass species composition, water depth, hydrodynamic energy, soil mud content (i.e., silt & clay $\Phi < 63 \mu m$) and the contribution of allochthonous C_{org} (Table 1). In particular, higher soil C_{org} deposits are usually found in meadows dominated by large seagrass species (Serrano et al., 2019), at relatively shallow depths (Serrano et al., 2014) and sheltered locations (Röhr et al., 2016; Samper-Villarreal et al., 2016), where fine sediment and allochthonous C_{org} accumulation is enhanced (e.g., close to other macrophytes, to river mouths or in urbanized areas) (Macreadie et al., 2012; Mazarrasa et al., 2017a, 2017b; Ricart et al., 2020) (Table 1).

At larger spatial scales, the magnitude and composition of seagrass soil C_{org} deposits have been related to the coastal geomorphic setting (estuarine vs. coastal) and bioregion (tropical vs. temperate), where particular

Table 2

Number of Unvegetated and Vegetated Soil Cores Included in This Study Based on Seagrass Genera Nested Within Species Size (Large, Small, and Unvegetated), Geomorphic Setting (Coastal and Estuarine), and Bioregion (Temperate Southern Ocean and Tropical Indo-Pacific)

Bioregion	Geomorphic setting	Size	Genera	# cores
Temperate Southern Ocean	Coastal	Large	<i>Amphibolis</i>	23
			<i>Posidonia</i>	77
			<i>Posidonia_Amphibolis</i>	13
		Small	<i>Halophila</i>	3
			<i>Zostera</i>	3
		Unvegetated		29
		Total		148
	Estuarine	Large	<i>Posidonia</i>	27
		Small	<i>Halophila</i>	9
			<i>Ruppia</i>	5
			<i>Zostera</i>	5
		Unvegetated		3
		Total		49
Tropical Indo-Pacific	Estuarine	Small	<i>Cymodocea</i>	5
			<i>Cymodocea_Halodule</i>	3
			<i>Cymodocea_Syringodium</i>	3
			<i>Halodule</i>	5
			<i>Halophila</i>	6
			<i>Ruppia</i>	3
			<i>Zostera</i>	11
		Unvegetated		7
		Total		43
		Total cores		240

environmental and climatic conditions modulate seagrass ecology, productivity, C_{org} mineralization rates and the accumulation of allochthonous C_{org} (Carruthers et al., 2002, 2007; Miyajima et al., 2015; Serrano et al., 2019; Short et al., 2007) (Table 1). Coastal meadows are usually exposed to greater hydrodynamic energy than estuarine meadows (Carruthers et al., 2002, 2007), which are more subject to inputs of terrigenous materials and anthropogenic impacts than coastal meadows (Kilminster et al., 2015). In coastal meadows, which develop in subtidal environments down to 40 m depth, light limitation of seagrass productivity is mainly due to depth (Duarte, 1991) and water turbidity, whereas in estuarine meadows, which occur in shallower depths, light limitation is influenced by water turbidity (Carruthers et al., 2002, 2007). Across climatic regions, tropical meadows are more exposed to higher temperatures, precipitation, and solar radiation than temperate meadows, as well as to extreme flooding and intense storms (Carruthers et al., 2002). High temperature favors soil C_{org} mineralization rates (Pedersen et al., 2011), while high precipitation regimes can enhance the accumulation of allochthonous C_{org} and fine sediment particles due to land run-off, but excess turbidity and low salinity negatively affect seagrass productivity (Chollett et al., 2007; Ridler et al., 2006). Finally, solar radiation may enhance seagrass productivity (Pollard & Greenway, 1993) but it can also reduce seagrass biomass if combined with high temperature and periods of exposure to air at low tide (Stapel et al., 1997).

Owing to the multiple factors that can influence soil C_{org} storage at different spatial scales, it is likely that soil C_{org} stocks and the main factors influencing these stocks vary in a spatial hierarchy across bioregions and geomorphic settings within bioregions. However, previous seagrass Blue Carbon studies have explored

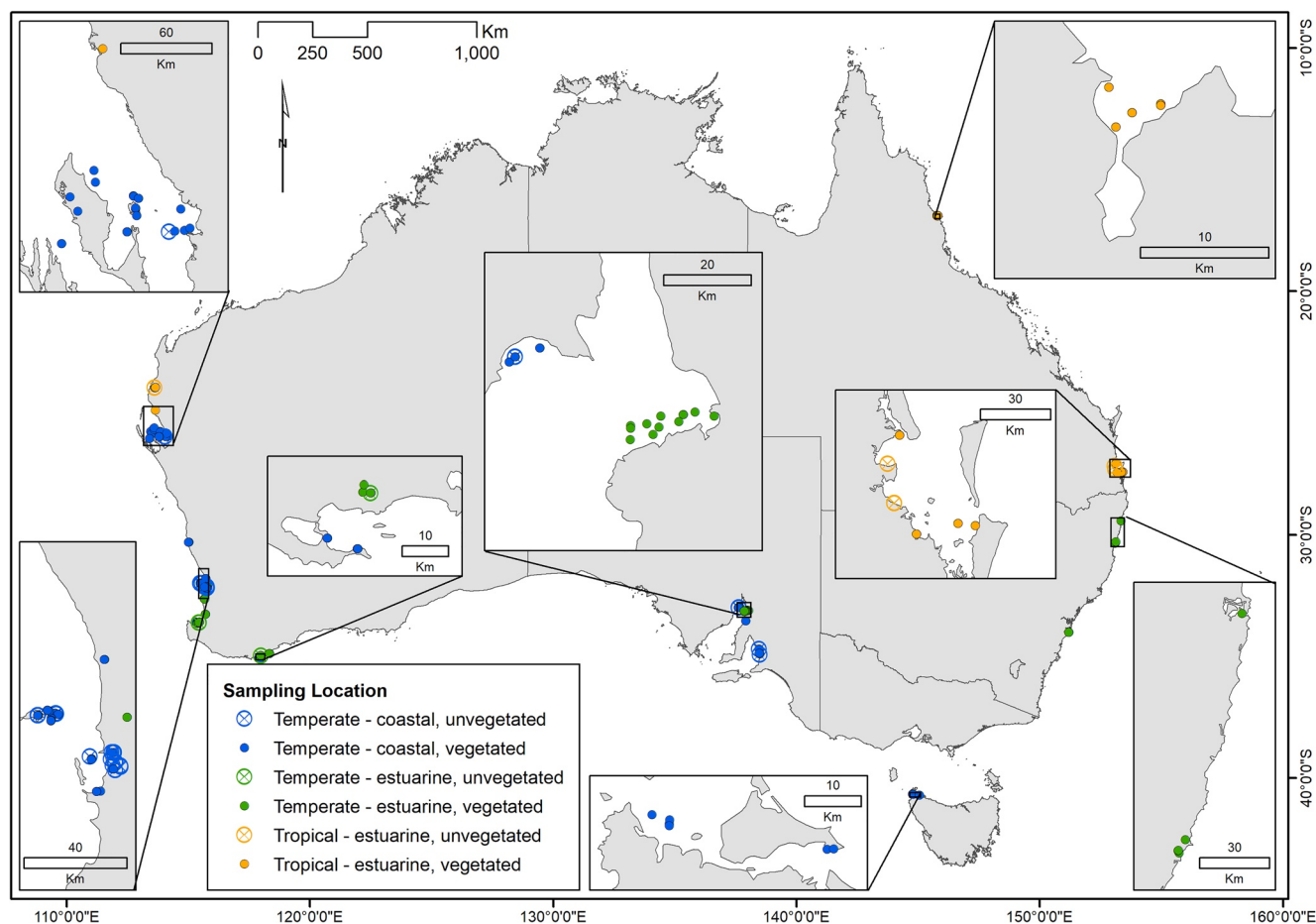


Figure 1. Sampling location of vegetated and unvegetated soil cores ($n = 240$) included in this study. The different colors represent the different seagrass environments studied: coastal geomorphic settings in the Temperate Southern Ocean (temperate-coastal), estuarine geomorphic settings in the Temperate Southern Ocean (temperate-estuarine), and estuarine geomorphic settings in the Tropical Indo-Pacific (tropical-estuarine).

the variability and drivers of soil C_{org} stocks within constrained spatial scales (e.g., meadow scale, coastal geomorphic settings or bioregion) independently (Ewers Lewis et al., 2020; Lavery et al., 2013; Miyajima et al., 2015; Oreska et al., 2017; Ricart et al., 2020; Serrano et al., 2019).

Here, we assess the variation in seagrass soil C_{org} stocks, composition, and drivers across bioregions and coastal geomorphic settings across Australia, which is an ideal continent to perform this large-scale study. It has the highest seagrass biodiversity in the world ($n = 33$ species out of the 61 species described worldwide (Kuo et al., 2018), inhabiting sheltered and exposed coastal areas and estuaries within tropical to temperate regions spanning 30° latitude (Carruthers et al., 2007; Kuo & McComb, 1989). Furthermore, Australia is recognized as a Blue Carbon hotspot, storing between 9% and 25% of the global seagrass meadow soil C_{org} stocks, yet the differences in soil C_{org} deposits and the drivers of those variations should be further explored (Serrano et al., 2019). Our study aims to assist in identifying the hotspot of seagrass carbon stocks for the implementation of Blue Carbon projects and to enhance the understanding of the critical environmental factors that need to be considered when planning Blue Carbon conservation or restoration projects while contributing to improved understanding of carbon cycling in seagrass meadows.

2. Materials and Methods

We compiled published (Serrano et al., 2019) and unpublished data on soil C_{org} concentration (%) and dry bulk density (DBD; $g\ cm^{-3}$) in the top 30 cm of 201 soils cores sampled in seagrass vegetated patches and 39 soil cores sampled in unvegetated patches (a total of 240 soil cores) distributed from 17°S to 41°S across Australia, growing from intertidal to 10 m water depth (Table 2, Figure 1). When possible, soil C_{org} isotopic signatures ($\delta^{13}C_{org}$, $n = 223$ cores) and fine sediment content data (% mud; $n = 128$ cores) were also compiled.

2.1. Factors Influencing Variability in Soil C_{org} Stocks

Soil cores were classified according to seagrass bioregions (Temperate-Southern Ocean and Tropical Indo-Pacific; Short et al., 2007) and geomorphic settings, as estuarine (i.e., located at the river mouth and/or influenced by river flow), or coastal (marine environment) (Table 2). Meadows were classified according to the size and life history traits of dominant species, considering those of the genera *Posidonia* and *Amphibolis* as large and persistent species, and those of the genera *Halodule*, *Halophila*, *Ruppia*, *Zostera*, *Cymodocea*, and *Syringodium* as small and opportunistic/colonizing species (Kilminster et al., 2015).

For each location where soil cores were sampled, the exposure to hydrodynamic energy was estimated using fetch against the dominant wind as a proxy. Fetch (km) was calculated with the “fetchR” package, using the Australian coastline shapefile from the GADM database (www.gadm.org, version 2.0) and the dominant wind for each location obtained from the Bureau of Meteorology (<http://www.bom.gov.au/climate/data/>). When sampled in the same location (i.e., 91 cores distributed across 24 different locations), cores shared the same fetch data. Fetch estimations were limited to coastal locations or outer estuarine locations due to the spatial resolution of the Australian coastline. As a result, fetch was estimated for a total of 223 soil cores.

Annual mean rainfall (years 1996–2005, 5 km resolution), annual mean air temperature (years 1995–2005, 5 km resolution), and annual mean solar radiation (years 1990–2011, 5 km resolution) for each location where soil cores were sampled were obtained from the Australian Bureau of Meteorology. Human pressure was estimated based on the intensity of land use, as “deviation from natural state,” using land use data from the Australian Bureau of Agriculture and Resource Economics and Sciences and adapting the methodology from Lenzen and Murray (2006).

2.2. Soil Organic Carbon Stocks

The collection and processing of the seagrass soil cores used in this study are described in detail in Serrano et al. (2019). C_{org} density ($g\ C_{org}\ cm^{-3}$) was estimated along the soil depth profile of each core by multiplying C_{org} concentration (%) by soil DBD ($g\ cm^{-3}$). For those cores where DBD was not available (in six cores), the average DBD of the seagrass soils compiled in this study ($1.06 \pm 0.02\ g\ cm^{-3}$) was used. Soil C_{org} stocks along the depth profile were estimated by multiplying the C_{org} density by the slice thickness. Soil C_{org} stocks in 30-cm thick soil deposits were estimated as the sum of C_{org} stock along the decompressed depth profile estimated using the compression factor, recorded during sampling by measuring the difference in surface soil elevation inside and outside the coring device (Gorham et al., 2021).

2.3. Statistical Analysis

We used general linear models (GLMs, distribution: normal, link function: identity) to examine differences in soil C_{org} stocks between seagrass and unvegetated sites for the whole database. For vegetated sites, GLMs were used to examine differences in soil C_{org} stocks between bioregions, and between coastal geomorphic settings and species size within the temperate region. The soil C_{org} stock data were square-root transformed before analysis to meet normality. Each soil core was treated as an independent replicate.

The contribution of potential C_{org} sources to the soil C_{org} stocks was assessed applying Bayesian Isotope Mixing Models with *simmr* and *rjags* packages in R (Parnell, 2016; Parnell et al., 2013) based on one tracer, the soil C_{org} isotopic signature ($\delta^{13}C_{org}$), and two potential sources, allochthonous C_{org} (derived from mangroves, tidal marshes, algae, and terrestrial inputs) and seagrass-derived C_{org} , as end-members in the

Table 3

Results of the General Linear Models (GLM) Applied to Test Differences in Soil C_{org} Stocks According to Patch Type (Vegetated vs. Unvegetated), Bioregion (Temperate Southern Ocean vs. Tropical Indo-Pacific), Geomorphic Setting (Coastal vs. Estuarine) Within the Temperate Southern Ocean Bioregion, Seagrass Size (Large vs. Small) Within Coastal Meadows, and Seagrass Size (Large vs. Small) Within Estuarine Meadows

Variables	GLM			
	<i>n</i>	Chi-square	<i>df</i>	<i>p</i> -value
Patch type (vegetated vs. unvegetated)	240	10.43	1	0.0012
Bioregion (tropical vs. temperate)	201	0.91	1	0.33
Geomorphic setting (estuarine vs. coastal) within the Temperate Southern-Ocean	165	0.78	1	0.38
Seagrass size (small vs. large) within coastal meadows	119	4.95	1	0.026
Seagrass size (small vs. large) within estuarine meadows	46	5.3	1	0.022

Note. Significant interactions are highlighted in bold ($p < 0.05$).

models. The isotopic signature of allochthonous and seagrass-derived C_{org} used in the models correspond to average $\delta^{13}C_{org}$ values measured in different seagrass meadows and estuarine macrophytes across Australia (Table S1). Terrestrial vegetation inputs, via riverine flow, typically have $\delta^{13}C_{org}$ values within the range of mangrove, tidal marsh, and algal values and so were not modeled as a separate source. The average $\delta^{13}C_{org}$ values obtained for the soil cores lay within the range defined by $\delta^{13}C_{org}$ values of allochthonous and autochthonous end-members (Figure S2). Isotope mixing models were run independently for vegetated and unvegetated sites, and for vegetated sites within each bioregion. In addition, independent isotope mixing

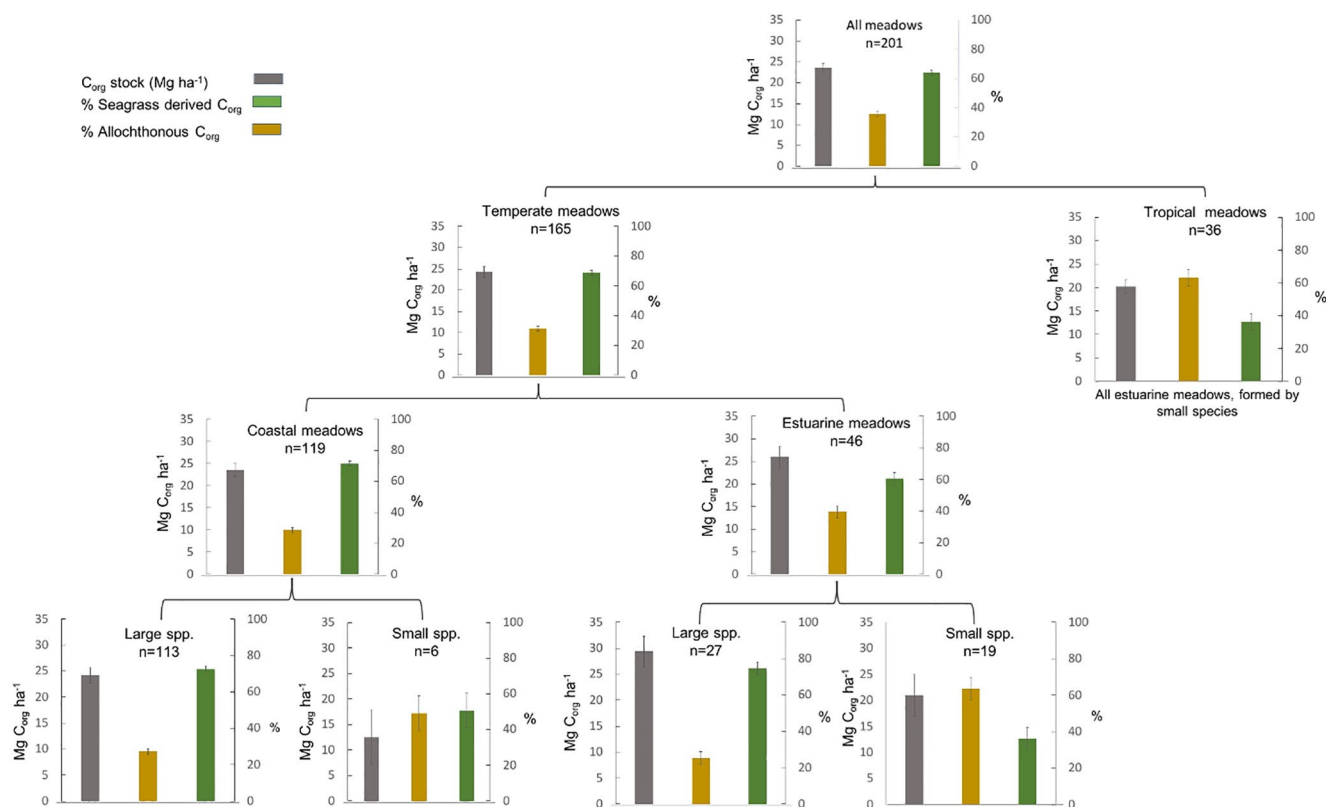


Figure 2. Seagrass soil C_{org} stocks (mean \pm SE $Mg C_{org} ha^{-1}$) (left y-axis) within the top 30 cm of soil, and contribution (%) of allochthonous and seagrass-derived C_{org} (mean \pm SD) (right y-axis) in the different seagrass environments examined at different spatial scales. The number of soil cores (n) for each category is indicated.

Table 4

Boosted Regression Tree (BRT) Models Performance Defined by R^2 and % Accuracy (Pearson Correlation), and the Variability Explained by Each Independent Variable (%) for Seagrass Soil C_{org} Storage Within Coastal Geomorphic Settings in the Temperate Southern Ocean, Estuarine Geomorphic Settings in the Temperate Southern Ocean, and Estuarine Geomorphic Settings in the Tropical Indo-Pacific

		BRT models		
		Temperate coastal	Temperate estuarine	Tropical estuarine
Performance	R^2	0.78	0.46	0.64
	Accuracy (%)	60	60	80
Variability explained by each independent variable (%) and their effect on soil C_{org} stocks	Species size	ns*	ns	Na
	Fetch (km)	17.8 ↓	2.8 –	51.2 ↓
	Mud (%)	33 ↑	NS	NS*
	$\delta^{13}C_{org}$ (‰)	15.7 ↑	46.7 ↑	1.4 ↓
	Meadow depth (m)	8.9 ↓	NS	NS
	Temperature (°C)	11.5 ↓	2.8 ↓	6.2 ↓
	Solar radiation ($MJ\ m^{-2}$)	3.8 ↑	38.7 ↓	13.9 ↑
	Rainfall (mm)	4.9 ↓	NS	27.3 ↓
	Deviation from natural state	4.3 –	9.1 ↓	NS

Note. The effect on soil C_{org} stocks of each variable is indicated as: ↑ for positive, ↓ for negative and “–” for variable for each model. * indicates variables where the number of data was too low to produce reliable results in the BRT analysis. NS = not significant, NA = not analyzed due to the low number of data available.

models were run for estuarine and coastal meadows within the temperate bioregion, and small and large species within each coastal geomorphic setting in the temperate bioregion.

The main drivers of soil C_{org} stocks were explored using boosted regression tree (BRT) analysis for the three seagrass environments represented in the database, defined by the combination of bioregion and habitat geomorphology type: coastal meadows within the Temperate-Southern Ocean (temperate-coastal, $n = 119$ cores, all subtidal), estuarine meadows within the Temperate-Southern Ocean (temperate-estuarine, $n = 46$, 41 subtidal, 5 intertidal) and estuarine meadows within the Tropical Indo-Pacific (tropical-estuarine, $n = 36$ cores, 22 subtidal, 14 intertidal). BRT is an ensemble method for modeling associations between response and explanatory variables. The BRT method utilizes a large number of relatively simple tree models to develop associations between response and explanatory variables and allows for more robust predictions. For fitting the BRT models, a learning rate of 0.001 was used and the interaction depth was specified at 5. To assess model performance and reduce overfitting by restricting the number of trees, we used a k-fold cross-validation method within R statistical software using the gbm package (Ridgeway, 2017). Performance was assessed through the calculation of the variability explained by the model (R^2) from the total mean deviance and residual mean deviance. In addition, a reserved data set (30% of data) which was not used in the creation of the models (i.e., 36 soil cores for temperate-coastal; 14 soil cores for temperate-estuarine and 11 soil cores for tropical-estuarine), was set aside to test the predictive accuracy of each model using Pearson correlation.

The independent variables considered in the models were species size, meadow depth, dominant wind fetch (km), solar radiation, temperature, total rainfall, the content of mud, the $\delta^{13}C_{org}$, and deviation from natural state. In the case of tropical-estuarine meadows, which were all formed by small species as no data from the tropical largest species (i.e., *Thalassia* or *Enhalus* spp.) were available, species size was excluded from the model.

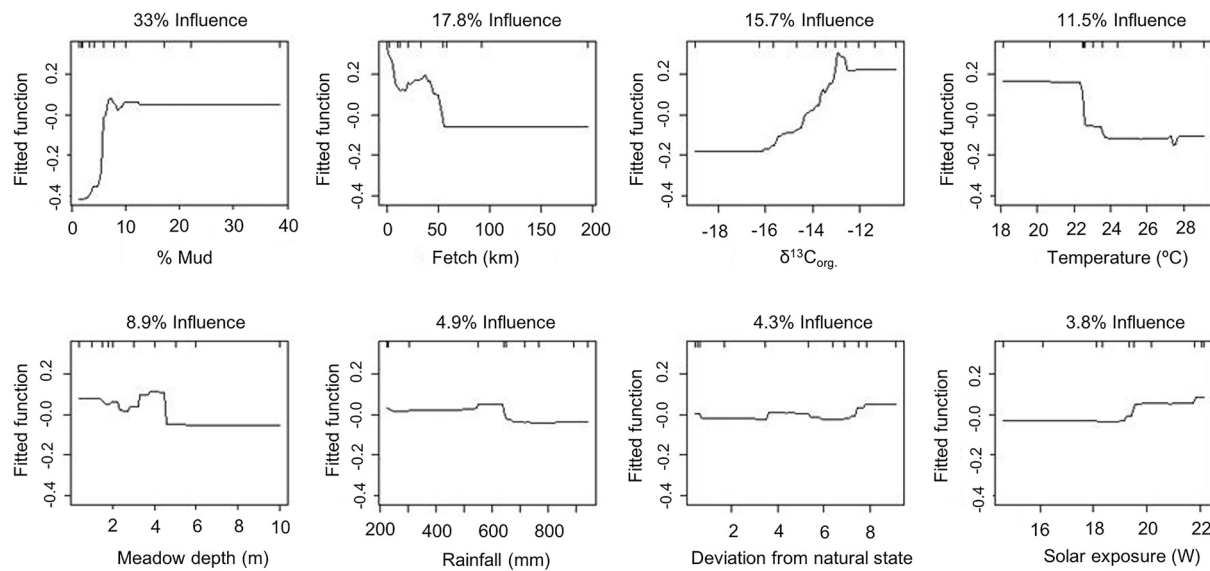


Figure 3. The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) model for soil organic carbon (C_{org}) in seagrass meadows from coastal environments within the Temperate Southern Ocean. Each graph represents the relationship between the variable and the fitted function from the BRT. All relationships are shown for the median values of the other variables in the model. The percentage influence of each variable on the full BRT is shown along the top of each graph, providing the relative contribution of each of the variables to the best BRT model as a percentage of the explained variance. Only variables with a significant effect are represented.

3. Results

3.1. Magnitude and Composition of Soil C_{org} Deposits

The vegetated and unvegetated soils examined stored $22.5 \pm 1.0 \text{ Mg } C_{org} \text{ ha}^{-1}$ (mean \pm SE) in the top 30 cm ($n = 240$). Soil C_{org} stocks were significantly higher in vegetated patches ($23.5 \pm 1.1 \text{ Mg } C_{org} \text{ ha}^{-1}$) than in unvegetated patches ($17.2 \pm 2.6 \text{ Mg } C_{org} \text{ ha}^{-1}$) (GLMs, $p < 0.01$) (Tables 3 and S3). Soil C_{org} stocks in temperate meadows and tropical meadows were similar ($24.3 \pm 1.3 \text{ Mg } C_{org} \text{ ha}^{-1}$ and $20.3 \pm 1.5 \text{ Mg } C_{org} \text{ ha}^{-1}$, respectively) (GLMs, $p = 0.3$) (Figure 2, Tables 3 and S3).

Within the temperate bioregion, coastal and estuarine meadows had similar soil C_{org} stocks (23.3 ± 1.5 and $25.9 \pm 2.4 \text{ Mg } C_{org} \text{ ha}^{-1}$, respectively) (GLMs, $p = 0.4$) (Figure 2, Tables 3 and S3), but in both the estuarine and coastal habitats, large species showed higher soil C_{org} stocks (29.4 ± 3.0 and $24.2 \pm 1.5 \text{ Mg } C_{org} \text{ ha}^{-1}$, respectively) than meadows formed by small species (21.0 ± 4.0 and $12.5 \pm 5.3 \text{ Mg } C_{org} \text{ ha}^{-1}$, respectively) (GLMs, $p < 0.05$).

Isotopic mixing models revealed that $64 \pm 2\%$ of the soil C_{org} stored in all vegetated sites examined was derived from seagrass, while $36 \pm 2\%$ was allochthonous. In unvegetated sites, $52 \pm 4\%$ was seagrass C_{org} and $48 \pm 4\%$ was allochthonous. The relative contribution of seagrass-derived C_{org} to the soil C_{org} pool varied across bioregions, coastal geomorphic settings, and species size (Figure 2, Table S3). Soil C_{org} stocks of temperate meadows were dominated by seagrass-derived C_{org} ($69 \pm 2\%$), whereas allochthonous C_{org} dominated in tropical meadows ($64 \pm 2\%$). Within the temperate region, seagrass-derived C_{org} constituted most of the soil C_{org} stocks in both coastal and estuarine meadows ($72 \pm 2\%$ and $61 \pm 4\%$, respectively). In meadows formed by large species, located in both estuarine and coastal areas, soil C_{org} stocks were dominated by seagrass-derived C_{org} ($75 \pm 4\%$ and $73 \pm 2\%$, respectively). In contrast, in temperate meadows formed by small species, C_{org} stocks were dominated by allochthonous C_{org} ($64 \pm 6\%$) in estuarine environments and showed similar contributions of seagrass ($51 \pm 10\%$) and allochthonous ($49 \pm 10\%$) C_{org} in coastal habitats.

3.2. Factors Influencing Variation in Soil C_{org} Stocks

All models had significant correlations between the observed SOC and the SOC predicted by the models ($p < 0.001$, Pearson correlation) (Table 4). The BRT model for tropical estuarine meadows showed the highest predictive accuracy at 80% whereas those for temperate coastal and temperate estuarine meadows

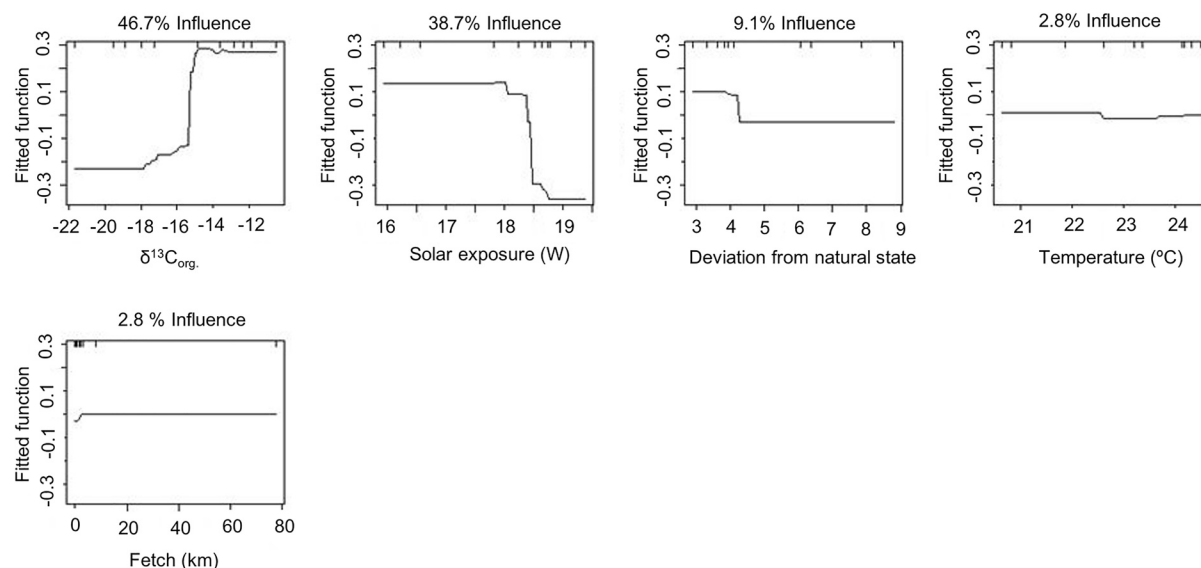


Figure 4. The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) model for soil organic carbon (C_{org}) in seagrass meadows from estuarine environments within the Temperate Southern Ocean. Each graph represents the relationship between the variables and the fitted function from the BRT. All relationships are shown for the median values of the other variables in the model. The percentage influence of each variable on the full BRT is shown along the top of each graph, providing the relative contribution of each of the variables to the best BRT model as a percentage of the explained variance. Only variables with a significant effect are represented.

showed predictive accuracy of 60% (Table 4). The BRT model developed for temperate-coastal meadows explained 78% of soil C_{org} stock variability while that for tropical-estuarine meadows explained 64% of the variability and that for temperate-estuarine meadows explained 46% of the variability (Table 4).

The BRT models showed that the contribution of each explanatory variable to the variability of soil C_{org} stocks differed among seagrass environments (Figure 3).

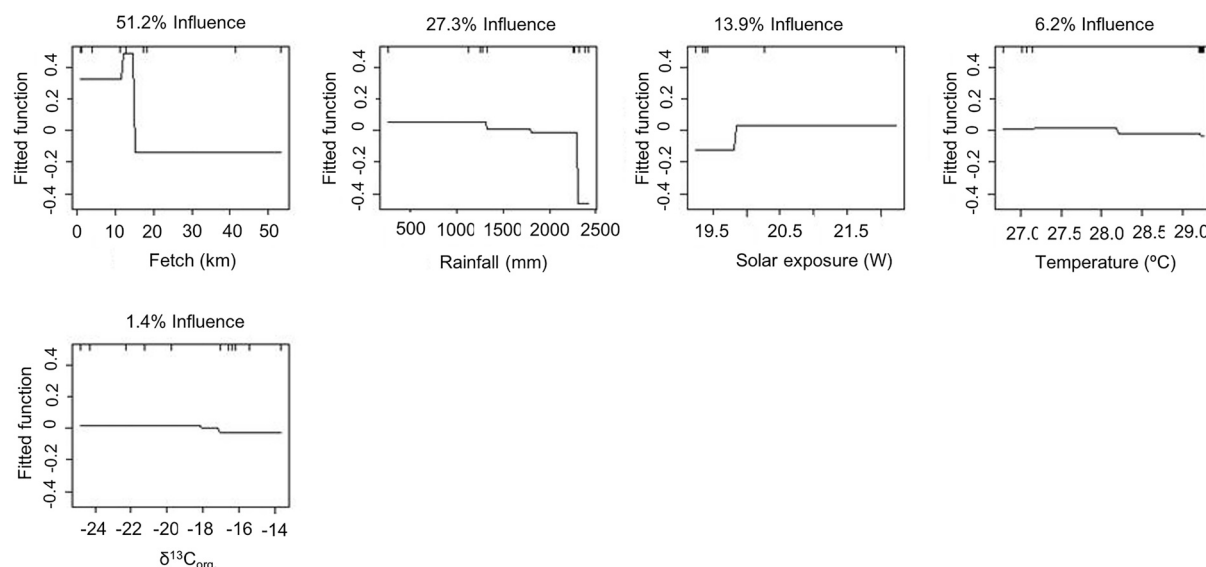


Figure 5. The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) model for soil organic carbon (C_{org}) in seagrass meadows from estuarine environments within the Tropical Indo-Pacific. Each graph represents the relationship between the variables and the fitted function from the BRT. All relationships are shown for the median values of the other variables in the model. The percentage influence of each variable on the full BRT is shown along the top of each graph, providing the relative contribution of each of the variables to the best BRT model as a percentage of the explained variance. Only variables with a significant effect are represented.

In temperate-coastal meadows, most of the variability in soil C_{org} stocks was explained by the mud content (33.0%), followed by the exposure to hydrodynamic energy (17.8%), the soil C_{org} isotopic signature ($\delta^{13}C_{org}$) (15.7%) and temperature (11.5%). All other potential drivers contributed to explain less than 10% of the variability in soil C_{org} stocks, with solar radiation and deviation from natural state showing the lowest contributions (3.8% and 4.3%, respectively) (Table 4; Figure 3).

In temperate-estuarine meadows, most of the variability in soil C_{org} stocks was explained by soil $\delta^{13}C_{org}$ (46.7%) and solar radiation (38.7%). All other drivers contributed to explain less than 10% of the variability in soil C_{org} stocks, with fetch and temperature showing the lowest contribution (2.8% in both cases) (Table 4; Figure 4).

For tropical-estuarine meadows, the exposure to hydrodynamic energy explained 51.2% of the variability in soil C_{org} stocks, followed by rainfall (27.3%) and solar radiation (13.9%) (Table 4; Figure 5). The other variables contributed to explain less than 10% of the variability in soil C_{org} stocks, with soil C_{org} isotopic signature contributing the least (1.4%).

The BRT models also showed different directional effects (i.e., positive, variable, or negative) on seagrass soil C_{org} stocks of the factors considered across bioregions and coastal geomorphic settings (Table 4; Figures 3–5). The exposure to hydrodynamic energy (i.e., fetch) had a negative effect on soil C_{org} stocks in temperate-coastal and tropical-estuarine meadows, but a variable effect in temperate-estuarine meadows. Water depth showed a negative effect in seagrass soil C_{org} stocks within temperate-coastal meadows but did not have an effect on temperate-estuarine nor in tropical-estuarine meadows. Higher temperature had a negative effect on soil C_{org} stocks in temperate-coastal and tropical-estuarine meadows, while in temperate-estuarine meadows temperature showed a variable effect. Solar radiation had a positive effect on soil C_{org} stocks of temperate-coastal and tropical-estuarine meadows, but a negative effect in soil C_{org} stocks of temperate-estuarine meadows. Precipitation had a negative effect on soil C_{org} stocks in temperate-coastal and tropical-estuarine meadows, but no significant effect in temperate-estuarine meadows. Deviation from natural state had a negative effect on soil C_{org} stocks in temperate-estuarine meadows, a variable effect in temperate coastal meadows, and no significant effect in tropical-estuarine meadows. Mud content had a positive effect on soil C_{org} stocks of temperate-coastal meadows, but no significant effect in temperate-estuarine and tropical-estuarine meadows. However, the low number of mud data available ($n = 6$) for tropical-estuarine meadows renders high uncertainties for this comparison (Table 4). The C_{org} isotopic signature ($\delta^{13}C_{org}$) was positively related to soil C_{org} stocks of temperate-coastal and temperate-estuarine meadows and a negatively related to soil C_{org} stocks in tropical-estuarine meadows.

According to the results of the BRT models, seagrass species size did not have a significant effect on soil C_{org} stocks for temperate-estuarine and temperate-coastal meadows (Table 4), contrary to results revealed by GLM analysis. In the case of temperate-coastal meadows, however, this result should be interpreted with care due to the low number of data available for small species ($n = 6$, Table 2).

4. Discussion

This study shows that at a continental scale, the magnitude of soil C_{org} deposits in seagrass soils was not different across bioregions and habitat geomorphic settings, but was higher in meadows dominated by large species compared to those dominated by small species. In contrast, the provenance (seagrass vs. allochthonous) of the soil C_{org} stocks differed across bioregions, geomorphic settings within each bioregion, and seagrass species size. The importance and effect of the climatic and environmental factors examined differed across seagrass environments (i.e., combination of coastal geomorphic settings and bioregion), showcasing complex synergistic and antagonistic interactions among factors driving seagrass soil C_{org} storage.

4.1. Magnitude and Provenance of Soil C_{org} Stocks

Soil C_{org} stocks in the top 30 cm of Australian seagrass meadows ($23.5 \pm 1.1 \text{ Mg } C_{org} \text{ ha}^{-1}$) were higher than those estimated for adjacent unvegetated patches ($17.2 \pm 2.6 \text{ Mg } C_{org} \text{ ha}^{-1}$) and contained 13% more seagrass-derived C_{org} , supporting the hypothesis that seagrass meadows act as natural C_{org} sinks (Miyaji-

ma et al., 2017; York et al., 2018). In addition, the large fraction of seagrass derived C_{org} found in adjacent unvegetated patches (contributing with 52% to the total soil stocks) suggests that seagrass meadows play a significant role as C_{org} sinks within and beyond their habitats through the export of seagrass-derived C_{org} (Duarte & Krause-Jensen, 2017).

The predominance of seagrass-derived C_{org} ($64 \pm 2\%$) in the seagrass soils studied, compared to previous studies (50% in Kennedy et al. [2010]) can be related to the predominance of data from large species ($n = 140$) over small species ($n = 61$). Large species are more effective at accumulating seagrass-derived C_{org} in soils than small species due to a higher below-ground biomass, larger detritus size, which reduces the available surface for microbial attack, and a higher content of recalcitrant components (Harrison, 1989; Serrano, Lavery, et al., 2016; Trevathan-Tackett et al., 2017a).

The magnitude of seagrass soil C_{org} deposits was not significantly different between bioregions. This contrasts with the expectation that the meadows within the Temperate-Southern Ocean region, which were predominantly formed by large, persistent species, would have larger soil C_{org} deposits than Tropical Indo-Pacific meadows, formed by small, colonizing/opportunistic species (Serrano et al., 2019; Short et al., 2007). The lack of difference among the bioregions may reflect the fact that the tropical meadows examined in this study were located in estuarine environments, where it is reasonable to expect high deposition of inorganic and organic particles transported by the river flow, leading to the formation of soil C_{org} deposits mainly dominated by allochthonous C_{org} ($64 \pm 5\%$), similar to results of previous studies (Miyajima et al., 2015; Ricart et al., 2020). These results indicate that in tropical-estuarine meadows formed by small species, the moderate contribution of seagrass biomass to the soil C_{org} pool may be compensated by a high accumulation of allochthonous C_{org} resulting in soil C_{org} stocks comparable to those developed in temperate meadows, dominated by larger species. We are unable to draw conclusions regarding tropical seagrass meadows in other habitats, such as the extensive meadows in the lagoons of the Great Barrier Reef (Coles et al., 2014), although the limited data for coral reef lagoon seagrasses available (one study including three water depths) suggests that their carbon stocks could be higher ($26\text{--}40 \text{ Mg } C_{org} \text{ ha}^{-1}$; York et al., 2018) than those reported here for tropical-estuarine meadows and temperate ones. In addition, we could not assess the effect of species size in tropical-estuarine environments as data from Australian *Thalassia* or *Enhalus* spp. meadows, the largest species in the tropical bioregion, were not available. However, estimates based on previous studies conducted in meadows formed by large species (i.e., *Thalassia* or *Enhalus* spp) in other tropical regions suggest a higher range of soil C_{org} stocks within the top 30 cm ($9\text{--}72 \text{ Mg } C_{org} \text{ ha}^{-1}$) than those found in this study for tropical meadows formed by small species ($5\text{--}46 \text{ Mg } C_{org} \text{ ha}^{-1}$) (Alongi et al., 2016; Asplund et al., 2020; Belshe et al., 2018; Githaiga et al., 2017). As the relative extent of *Thalassia* and *Enhalus* spp. compared to other tropical species in Australia is unknown, the implications of not including them in our study are not possible to assess. To overcome these limitations in our analysis, further sampling of tropical meadows, including meadows formed by large tropical seagrass species (i.e., *Thalassia* and *Enhalus* spp.) in this bioregion and in offshore locations is warranted, particularly given the potentially extensive area of offshore tropical meadows (Mckenzie et al., 2020).

Within the temperate bioregion, both coastal and estuarine meadows, dominated by large species, showed similar soil C_{org} stocks mostly composed of seagrass-derived C_{org} ($71.5 \pm 1.7\%$ and $60.5 \pm 3.8\%$, respectively). Yet, the size of the species influenced the magnitude and composition of soil deposits in both types of geomorphological settings. Meadows comprising of large species had larger soil C_{org} stocks than small species and were mainly composed of seagrass-derived C_{org} , in both temperate estuarine and temperate coastal meadows, reflecting their higher and more refractory biomass (Gullström et al., 2018; Serrano, Lavery, et al., 2016; Trevathan-Tackett et al., 2017a). In contrast, soil C_{org} deposits in meadows dominated by small species had a higher dependency on allochthonous inputs, which contributed $64 \pm 6\%$ of C_{org} stocks in temperate estuarine meadows and 50% of C_{org} stocks in temperate coastal environments. A similarly high abundance of allochthonous C_{org} inputs has been noted for small species meadows elsewhere (Miyajima et al., 2015). As a consequence, Australian meadows formed by smaller species contained nearly two times higher soil C_{org} deposits in estuarine meadows ($21 \pm 4 \text{ Mg } C_{org} \text{ ha}^{-1}$ and $20 \pm 2 \text{ Mg } C_{org} \text{ ha}^{-1}$, in temperate and tropical bioregions, respectively) than in coastal meadows ($13 \pm 5 \text{ Mg } C_{org} \text{ ha}^{-1}$). These results highlight the importance of riverine and terrestrial inputs in the formation of soil C_{org} deposits in meadows comprised of small seagrass species (Miyajima et al., 2015). In contrast, in meadows formed by large species,

where most of the C_{org} is of seagrass origin (Serrano, Lavery, et al., 2016), soil C_{org} stocks were more similar in coastal and estuarine environments ($24 \pm 2 \text{ Mg } C_{org} \text{ ha}^{-1}$ and $29 \pm 3 \text{ Mg } C_{org} \text{ ha}^{-1}$, respectively).

4.2. Factors Determining Soil C_{org} Stocks Across Bioregions and Geomorphological Settings

The BRT models revealed that factors driving soil C_{org} stock variability differed across seagrass environments and showed different effects (i.e., positive, variable, or negative) in the soil C_{org} stocks (Table 4; Figure 4) highlighting the need of considering specific conditions at the landscape scale for Blue Carbon projects.

In temperate coastal meadows, the soil C_{org} stocks were positively associated with mud content and $\delta^{13}C_{org}$, and negatively associated with hydrodynamic exposure (Table 4). These results demonstrate that, within temperate-coastal areas, soil C_{org} stocks tend to be higher in meadows inhabiting sheltered bays compared to areas exposed to waves and currents, as in sheltered locations sedimentation is enhanced and sediment erosion and seagrass detritus export is reduced, resulting in seagrass soils enriched in organic matter and fine sediment particles compared to more exposed locations (Novak et al., 2020; Röhr et al., 2016). The accumulation of mud enhances C_{org} preservation by reducing oxic conditions and protecting organic particles from mineralization (Burdige, 2007; Mayer, 1994), contributing to the positive relationship found between the content of mud and soil C_{org} stocks in this environment, which is consistent with previous studies (Dahl et al., 2016; Miyajima et al., 2017). The positive relationship between soil C_{org} and $\delta^{13}C_{org}$ reflects the dominance of meadows formed by large species in this environment (95% of the cores) and is consistent with findings by Serrano, Lavery, et al. (2016) that attributed this relationship to the high efficiency of large species at storing seagrass-derived C_{org} in the soil compartment due to their large below-ground biomass. However, contrary to our results, the positive relationship between mud content and soil C_{org} stocks found in Serrano, Lavery, et al. (2016) was restricted to meadows formed by small species whereas no significant relationship was found for large species, where a high proportion of the C_{org} is of autochthonous origin and C_{org} stocks do not depend as much on particle sedimentation from the water column. We attribute this difference in the results to the fact that the analysis by Serrano, Lavery, et al. (2016) included coastal and estuarine environments for meadows dominated by large species. In contrast, our results are based only on coastal meadows, where the high hydrodynamic energy also constraints the accumulation and preservation of autochthonous C_{org} derived from large species biomass (in addition to allochthonous C_{org}) by favoring erosion and export. Thus, in these high hydrodynamic environments, mud content is positively related to C_{org} content also in meadows formed by large species. The results found in this study suggest that, in temperate coastal areas, soil C_{org} stocks tended to decrease as meadow depth increased (Table 4), likely due to the decrease in seagrass productivity and biomass in response to reduced irradiance with depth as observed for the species of *Posidonia* in Australia and other seagrasses species elsewhere (Alcoverro et al., 2001; Collier et al., 2007). However, the decrease in seagrass soil C_{org} as meadow depth increases has been mainly observed in meadows formed by large species (Serrano et al., 2014) whereas in meadows formed by small species, where the contribution of seagrass-derived C_{org} is already minor compared to allochthonous C_{org} , this trend is not always observed (York et al., 2018). High levels of solar radiation can compensate the irradiance limitation in subtidal conditions, which explains the increase in soil C_{org} stocks with increasing solar radiation in temperate coastal meadows observed in the BRT models (Table 4). In contrast, soil C_{org} stocks were negatively related to precipitation (Table 4), as rainfall enhances turbidity, which can constrain seagrass productivity (Chollett et al., 2007; Ridler et al., 2006), particularly in the case of temperate coastal meadows, where subtidal conditions already limit irradiance. Surprisingly, deviation from natural state had no clear effect in soil C_{org} stocks in temperate-coastal meadows (Table 4) possibly because the relatively high hydrodynamic energy might reduce the exposure of meadows to the input of nutrients, organic matter, and other pollutants, that usually occur in areas with high levels of human modifications (Bowen & Valiela, 2001).

In temperate-estuarine meadows, most of the variability in soil C_{org} stocks was explained by the $\delta^{13}C_{org}$ (46.7%) and solar radiation (38.7%), which had a positive and a negative effect, respectively (Table 4). The positive relationship with $\delta^{13}C_{org}$ is consistent with the high abundance of large species among the meadows examined, where the formation of soil C_{org} deposits is more dependent on seagrass productivity than on the accumulation of allochthonous C_{org} (Serrano, Lavery, et al., 2016). In this seagrass environment, increasing solar radiation showed a negative effect on the soil C_{org} stocks. The negative effect of increased solar radiation on soil C_{org} stocks could be related to the negative impacts of intense solar radiation on seagrass cover and biomass (Seddon

et al., 2000), particularly in combination with high temperatures in intertidal and shallow subtidal conditions. The lack of significant effects of many of the other potential explanatory variables in temperate estuarine meadows (Table 4) likely reflects the nature of estuarine environments which are exposed to low hydrodynamic conditions, mainly derived from wind and tides, compared to coastal meadows (Kilminster et al., 2015). Meadow depth did not affect soil C_{org} stocks in temperate-estuarine meadows (Table 4), probably because most of these meadows occur in very shallow waters (intertidal to 4 m, but generally only to about 2 m), where the effect of decreasing irradiance with depth is less severe than in coastal meadows that typically distribute along a larger and deeper depth range in Australia (0.5–10 m). Increasing rainfall did not influence soil C_{org} stocks in temperate-estuarine meadows (Table 4), suggesting that the precipitation regime in this bioregion may not lead to critical turbidity conditions for shallow estuarine meadows, which is in contrast to what was found for deeper temperate-coastal meadows in this study. In temperate-estuarine meadows, deviation from natural state showed a negative effect in soil C_{org} stocks (Table 4), reflecting the higher influence of human activities in estuarine meadows compared to coastal areas (Kilminster et al., 2015). This is particularly the case in bar-built estuaries characteristic of the Australian temperate region, which in our study represents nearly half (5 out of 11) the temperate estuaries included. Bar-built estuaries in temperate Australia have experienced most of the coastal development since European settlement in the 1800s in Australia and are permanently closed or only intermittently open, resulting in reduced flushing and the potential for greater impacts from pollution (Brearley, 2005).

In tropical-estuarine meadows, soil C_{org} stocks were mainly driven by fetch, precipitation, and solar radiation (Table 4, Figure 3). In this environment, where seagrass meadows are formed by small species and soil C_{org} deposits are formed mainly by allochthonous C_{org} , hydrodynamics play a significant role in the formation of C_{org} deposits, which are typically larger in sheltered and depositional environments compared to more exposed ones (Samper-Villarreal et al., 2016). In meadows formed by small species, soil C_{org} stocks are usually directly related to mud content (Serrano, Ricart, et al., 2016), but the low number of data on mud content for tropical-estuarine meadows did not allow us to assess the relationship between mud content and soil C_{org} stocks for the meadows examined (Table 4). Similar to temperate-estuarine meadows, in tropical-estuarine environments, seagrass soil C_{org} stocks were not influenced by water depth (Table 4) as meadows develop in shallow areas (from the intertidal to 1 m depth) where irradiance is limited by the high water turbidity caused by periodic extreme flood and cyclonic events (Carruthers et al., 2002). Thus, greater precipitation within the tropical bioregion showed a negative effect on soil C_{org} stocks (Table 4), as it usually leads to extreme turbidity conditions that constraint seagrass productivity and can cause periodic declines of seagrass cover and density (Chollett et al., 2007; Ridler et al., 2006). In tropical-estuarine meadows, increased solar radiation may compensate for the lower irradiance due to high turbidity, which may explain the positive effect of solar radiation on soil C_{org} stocks found (Table 4). Deviation from the natural state did not affect soil C_{org} stocks of tropical-estuarine meadows, unlike temperate estuaries (Table 4). This could be because most of the cores within the tropical region were located in relatively remote areas with low anthropogenic influence, compared to the temperate-estuarine meadows, which were generally located close to large cities. In addition, most of the tropical-estuarine cores analyzed are in permanent open estuaries with continuously flowing rivers (Carruthers et al., 2002), reducing the exposure of seagrass meadows to anthropogenic inputs compared to meadows located in bar built-estuaries.

In all seagrass environments analyzed, soil C_{org} stocks were negatively related to temperature although the magnitude of the effect was higher in temperate-coastal meadows (11.5% variability explained by temperature) compared to tropical-estuarine meadows and temperate-estuarine meadows (6.2% and 2.1% of the variability explained, respectively). This difference is likely attributed to the broader range of temperatures encompassed by the temperate coastal meadows studied (19 °C – 29 °C) compared to that of tropical-estuarine meadows (27 °C– 29 °C) and temperate-estuarine meadows (21 °C –25 °C) (Figures 3–5). Although warmer temperatures enhance seagrass photosynthetic rates, when a thermal optimum is surpassed, stress responses lead to increased respiration rates and a decrease in net primary productivity (Lee et al. 2007). In addition, degradation and remineralization of seagrass detritus is enhanced under higher temperatures and aerobic conditions (Ainley & Bishop, 2015; Trevathan-Tackett et al., 2017b)

Although large species were found to store larger soil C_{org} stocks than small species in the temperate-coastal and temperate-estuarine meadows examined, the BRT models revealed that species size *per se* did not significantly contribute to explaining the variability in soil C_{org} stocks when other factors are considered (Table 4). In particu-

lar, in temperate-coastal meadows and temperate-estuarine meadows, the influence of species size in soil C_{org} stocks was better explained by the $\delta^{13}C_{org}$ (Table 4), which depends on the relative inputs of seagrass biomass (higher in large species than in small species) versus allochthonous material, over which other factors, such as the exposure to hydrodynamic energy (in the case of temperate-coastal meadows), act. These results highlight the complex interactions among biotic and abiotic factors that govern the formation of seagrass soil C_{org} deposits.

5. Conclusions

Soil C_{org} stocks across Australian seagrass meadows were found to be similar between bioregions and coastal and estuarine settings but larger seagrass species had higher soil C_{org} stocks than small species. In contrast, the origin of the C_{org} stored in seagrass soils and the factors determining the formation of soil C_{org} deposits differed across bioregions, coastal geomorphic settings within the temperate bioregion, and seagrass size. The findings that bioregion and geomorphic setting are not necessarily good predictors of soil C_{org} stocks argue against the use of broad regional or geomorphic-based averages for predictions of potential carbon abatement or avoided emissions following seagrass conservation and restoration efforts. Instead, site-specific estimates based on the local environmental factors should be considered and embedded into models for carbon inventories and greenhouse gases accounting purposes.

Data Availability Statement

Data used in this manuscript are published online (Mazarrasa et al. 2020) and can be accessed at <https://ro.ecu.edu.au/datasets/53/>.

Acknowledgments

This project was supported by the CSIRO Marine and Coastal Carbon Biogeochemical Cluster, CSIRO Oceans and Atmosphere, the ECU Faculty Research Grant Scheme and Early Career Research Grant Scheme, and the Australian Research Council (DE170101524, DP200100575, LP160100242). Inés Mazarrasa was funded by a Juan de la Cierva formation post-doc fellowship from the Ministerio de Ciencia, Innovación y Universidades (Spanish Government) and by a José Castillejo fellowship from the Ministerio de Educación, Cultura y Deporte (Spanish Government). Anna Lafratta was supported by Holsworth Wildlife Research Endowment-Equity Trustees Charitable Foundation (G1003426). Oscar Serrano was supported by an ARC DECRA (DE170101524). Stacey Trevathan-Tackett was supported by Deakin University's ADPR Fellowship.

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